

BIOSYSTEMATIC STUDIES OF *PHACELIA CAPITATA*
(HYDROPHYLLACEAE), A SPECIES ENDEMIC TO
SERPENTINE SOILS IN SOUTHWESTERN OREGON

J. STEPHEN SHELLY¹

Department of Botany and Plant Pathology,
Oregon State University, Corvallis, OR 97331

ABSTRACT

Studies of the distribution, edaphic restriction, cytology, and morphology of *Phacelia capitata* were undertaken to assess the relationship of the species within the *Phacelia magellanica* polyploid complex. *Phacelia capitata* is restricted to serpentine or related substrates in Coos, Douglas, and Jackson counties in southwestern Oregon. Chromosome counts of $n=11$, the base number for the complex, were obtained from 19 of 20 populations sampled. Two populations contained tetraploid ($n=22$) individuals, one of these being a mixed population of diploids and tetraploids. Morphological studies uphold the distinctiveness of *P. capitata* at the diploid level. The origin of the tetraploids is problematic, but some specimens suggest that *P. capitata* has hybridized in the past with *P. heterophylla* ssp. *virgata* and plants resembling *P. hastata*. Owing to their scarcity and geographic restriction these hybridization events appear to have been recent, and they do not challenge the status of *P. capitata* as one of the most morphologically and ecologically distinct members of the *P. magellanica* complex. The species appears to be an example of an edaphic neoendemic.

Ultramafic soils are those derived from the igneous rocks peridotite and dunite and their metamorphic derivative, serpentinite. The spectacular influences that these substrates have on the plants that inhabit them are well known, and are of great interest to community ecologists and biosystematists. Serpentine vegetation is frequently dwarfed, and xerophytism is common. Species composition is often unique, and endemism and range disjunction are characteristic of serpentine floras (Kruckeberg 1969, 1984; Whittaker 1954, 1960).

In southwestern Oregon, serpentine substrates occur over large areas in Curry and Josephine counties, and in smaller and more widely scattered outcrops to the north and east in Coos, Douglas, and Jackson counties (Fig. 1). *Phacelia capitata* Kruckeberg is restricted to the northeasternmost serpentine outcrops in this region.

Phacelia capitata is a member of the *P. magellanica* (Lam.) Cov. polyploid complex, a wide-ranging group of biennial and perennial species having affinities with the South American species *P. secunda* Gmel. (= *P. magellanica*). The members of this polymorphic group

¹ Present address: Montana Natural Heritage Program, State Library, 1515 E. 6th Avenue, Helena, MT 59620.

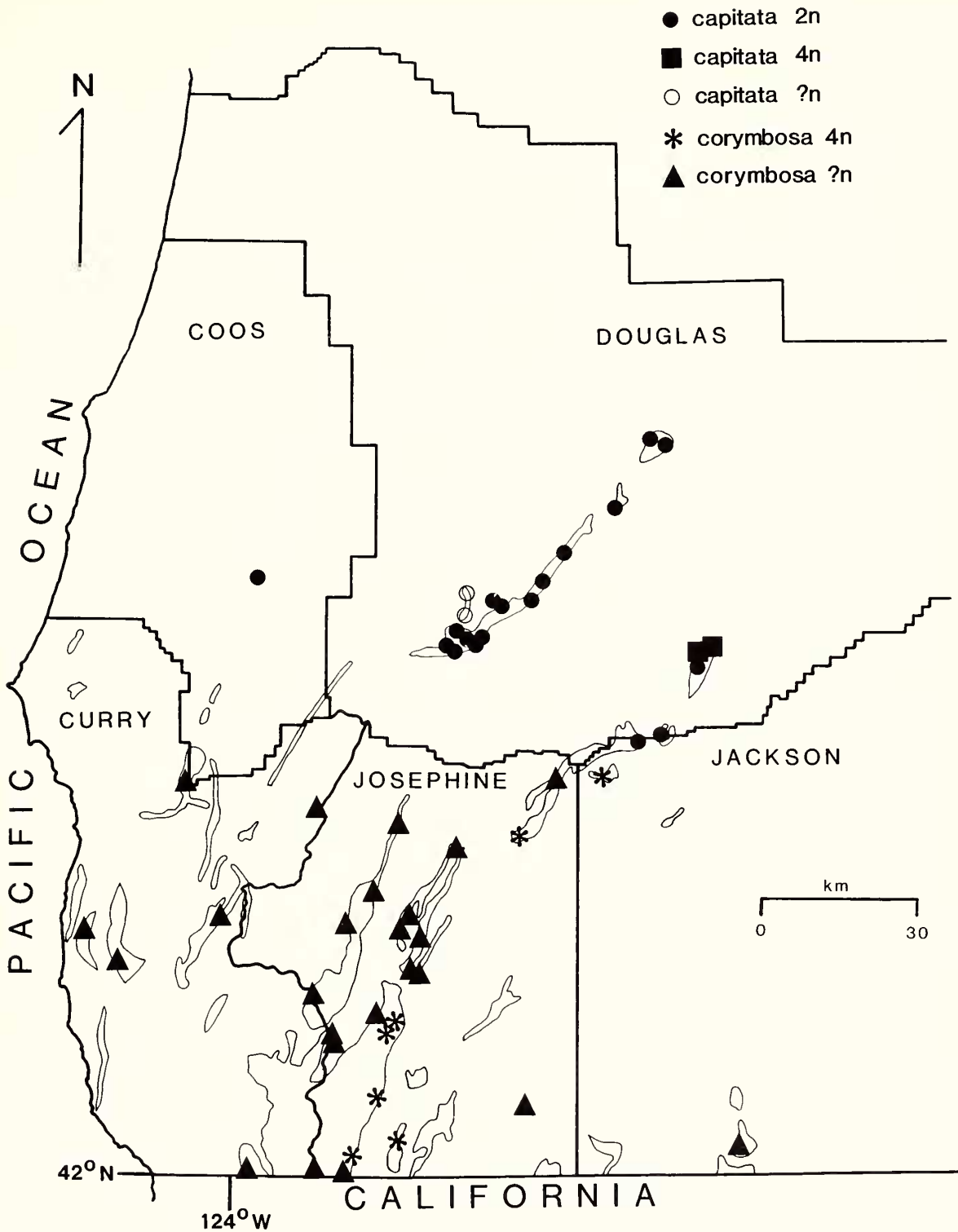


FIG. 1. Geographic distribution and chromosome numbers of *Phacelia capitata* and *P. corymbosa* in southwestern Oregon. Ultramafic formations are outlined (Wells and Peck 1961). *Phacelia corymbosa* locations are plotted from herbarium specimens housed at OSC, except for the tetraploid location at Sexton Mountain, Josephine County (Heckard 1960).

form a polyploid pillar complex (Stebbins 1971) that has a foundation comprising seven species with a base chromosome number of $x=11$, including *P. capitata* (Heckard 1960 and pers. comm.). The latter was described by Kruckeberg (1956). In his detailed study,

however, Heckard (1960) did not assess the interrelationships of *P. capitata* within the *P. magellanica* complex.

Owing to its restriction to serpentine soils (or closely similar derivatives) over a small geographic area, *P. capitata* has received attention as a potentially threatened species. Most recently it has been placed on the "watch list" of Oregon rare, threatened, and endangered plant species (Oregon Natural Heritage Data Base 1987). In addition, the species is a Category 2 federal candidate, under review for possible listing by the U.S. Fish and Wildlife Service (U.S. Department of Interior 1985).

My study was undertaken to assess the distribution, edaphic restriction, cytology, and morphological characteristics of *P. capitata*. I also studied natural populations of other species in the complex that occur in southwestern Oregon (*P. corymbosa* Jepson, *P. hastata* Douglas ex Lehmann, and *P. heterophylla* Pursh), to evaluate the interrelationships of *P. capitata* within the *P. magellanica* complex.

METHODS

Distribution. I compiled locations for 13 *P. capitata* populations from specimens deposited at various herbaria (CAS/DS, HSC, JEPS, ORE, OSC, UC, and WTU), from the Oregon Rare, Threatened, and Endangered Plant files housed in OSC, from U.S. Bureau of Land Management offices in Roseburg and Medford, Oregon, and from the Oregon Natural Heritage Data Base in Portland. My field studies were conducted during May–July 1982, April 1983, and April–June 1984. I surveyed as many locations as possible, in both serpentine and non-serpentine areas of southwestern Oregon, to determine the location and status of *P. capitata* populations.

Edaphic restriction. To characterize the edaphic environment of the ultramafic areas occupied by *P. capitata*, I collected soil samples from four fully serpentinized locations, and from one less serpentinized site. In addition, I sampled two serpentine locations for *P. corymbosa*, and one non-serpentine location for *P. heterophylla*. The soil analyses were conducted by the Soil Testing Laboratory at Oregon State University, using the extraction and analysis methods of Berg and Gardner (1978).

Cytology. Chromosome counts were made from pollen mother cells. Immature helicoid cymes were field-fixed in a mixture of 3 parts 95% ethanol : 1 part glacial acetic acid (V:V) for 24 hours. They were then washed in two overnight changes of 70% ethanol, and frozen in a third change of the same. After warming at 55–60°C for 24–48 hours in an alcoholic hydrochloric acid-carmin stain (Snow 1963), the cymes were rinsed in distilled water and studied immediately, or stored in 70% ethanol in a freezer. Anthers were dissected

onto slides, squashed in 45% acetic acid, and semi-permanently mounted.

Morphological studies. A total of 530 living individuals from 26 natural populations in southwestern Oregon was studied. For *P. capitata*, 420 plants from 20 populations were examined. For comparison with *P. capitata*, 110 plants representing other members of the *P. magellanica* complex were studied: 80 of *P. corymbosa* (4 populations), 20 of *P. heterophylla* ssp. *virgata* (E. Greene) Heckard (1 population), and 10 of *P. hastata* (1 population).

Data for 10 morphological characteristics were collected from each plant studied: blade length (mm), leaf width (mm), width of corolla opening (mm), corolla length (mm), calyx length (mm), stem height (cm), number of leaf lobes, number of floral branches below the terminal cymes, type of leaf lobing, and glandulosity. The five leaf and flower characters were measured with a Zeiss 10× handlens containing a 10 mm scale. Stem height was measured from the base of the flowering stem to the tip of the terminal cymes. Qualitative assessments of the type of leaf lobing and the degree of glandulosity were made in the following manner:

Type of leaf lobing

0—leaves entire.

1—leaves pinnatifid (lobes with a broad base at the midvein).

2—leaves pinnately compound (lobes reaching the midvein, with entire leaflets distinguishable).

Glandulosity (when viewed with 40× Zeiss dissecting microscope)

0—eglandular.

1—a few scattered glandular trichomes among the longer tapering trichomes, mainly in and near the inflorescence.

2—densely and conspicuously glandular, especially on intermediate-length trichomes in and near the inflorescence, on the pedicels, and on calyces.

The mean values for each of the ten morphological characteristics were calculated for each population and subjected to a cluster analysis using CLUSTER, a hierarchical, agglomerative, combinatorial program (Keniston 1978). The Bray-Curtis dissimilarity index was used, and the data were standardized using division by the attribute maximum, in which all values for a given morphological attribute are divided by the maximum value observed for that attribute. This removes “high score bias,” and allows use of quantitative and qualitative values together. A group average fusion strategy was used; this method produces only moderately sharp clustering, but more directly reflects the relationships originally expressed by the dissimilarity measure (Boesch 1977).

I compared the stem vestiture of *P. capitata* with that of *P. cor-*

ymbosa, another serpentine member of the *P. magellanica* complex, using scanning electron microphotographs prepared by the Oregon State University Scanning Electron Microphotography Lab.

RESULTS

Distribution. Twenty-two extant populations of *P. capitata* were located and studied (Table 1, Fig. 1). These populations are associated with the northeasternmost serpentine outcrops in southwestern Oregon, in central and southwestern Douglas, southern Coos, and northwestern Jackson counties (Fig. 1). The populations are generally located on slopes with southerly exposures, and occur at elevations from 100 to 1460 m.

Six populations of *P. corymbosa*, two of *P. heterophylla* ssp. *virgata*, and one of *P. hastata* were also studied (Table 1). At only one location was *P. capitata* found growing in biotic sympatry with any other member of the *P. magellanica* complex; at the Boomer Hill (west) site in Douglas County (the "sub-serpentine" location), it occurs along a disturbed road bank in a mixed population with the plants identified herein as *P. hastata*.

Edaphic restriction. Table 2 presents the results for eight soil analyses. Soils at the Boomer Hill (west) site (*P. capitata* and *P. hastata*) appear to be derived from metamorphic rocks similar to serpentine, but darker blackish-orange in color. The Tiller sample is from a non-serpentine area adjacent to the serpentine outcrops along Elk Creek in Douglas County. The remaining six samples are for soils derived from fully serpentinized parent materials; the rocks are a shiny, deep greenish-black color.

The serpentine soils are all characterized by low levels of phosphorus and low Ca/Mg ratios; these properties have been well-documented (Kruckeberg 1984; Proctor and Woodell 1975). The sub-serpentine sample has a higher Ca/Mg ratio than the more typical serpentine soils, but it is within the range of values reported by Proctor and Woodell (1975) for such soils.

Although large amounts of iron are often found in serpentine soils (Proctor and Woodell 1975), the results do not indicate this for the samples obtained in my study. The highest concentrations of iron are found in the sub-serpentine and non-serpentine samples.

The remaining analyses (pH, K, Cu) do not indicate any consistent differences between the serpentine and non-serpentine samples. Serpentine soils from the *P. capitata* and *P. corymbosa* sites are similar in chemical composition.

Cytology. At 19 of 20 sites, *P. capitata* occurs at the base (diploid) chromosome level of $n=11$ (Table 1). Of particular interest are the Elk Creek and Callahan Creek populations, both of which contain

TABLE 1. STUDY POPULATIONS AND CHROMOSOME NUMBERS FOR THE *PHACELIA MAGELLANICA* COMPLEX, SOUTHWESTERN OREGON. All collection numbers are those of the author (JSS), except where noted. Voucher specimens are deposited in the Oregon State University Herbarium (OSC). Site names denote approximate locations; specific data are available from the author. An asterisk indicates a representative voucher from the same population, the actual chromosome count having been obtained from a separate, unvouchered individual.

P. capitata Kruckeberg. $n=11$ —OR, Coos Co.: Bridge, *A. Kruckeberg* 2703 (WTU, isotype). Douglas Co.: Beatty Creek, 419; Bilger Creek, *JSS and M. Nelson* 724; Boomer Hill (W), *JSS and R. Holmes* 766; Boomer Hill (E), *JSS and R. Holmes* 781; Cow Creek (central), 405; Cow Creek (W), 411; Cow Creek (E), 681; Doe Creek, 706; The Drew, *JSS and M. Nelson* 734*; Elk Creek, *JSS and M. Nelson* 726; Lee Creek, 399; Little River, 690*; Myrtle Creek (N), 414; Peel, 354*; SW flank of Red Mountain, *JSS and M. Nelson* 736; Salt Creek, *JSS and M. Nelson* 725*; Weaver Road, 689. Jackson Co.: Goolaway Gap, *JSS and M. Nelson* 738.

P. capitata Kruckeberg. $n=22$.—OR, Douglas Co.: Callahan Creek, 440; Elk Creek, *L. Heckard* 2930 (JEPS), *JSS* 433.

P. capitata Kruckeberg. Chromosome number unknown—OR, Douglas Co.: Doe/Thompson Ridge, *JSS and R. Holmes* 783; Rice Creek, *JSS and R. Holmes* 792.

P. corymbosa Jepson. $n=22$ —OR, Jackson Co.: Grave Creek, 441. Josephine Co.: Eight Dollar Mountain (S), 700; Eight Dollar Mountain (N), 702; Rough and Ready Creek, 698; Waldo, 697; Wimer Road, *L. Constance and R. Bacigalupi* 3394 (WTU).

P. hastata Douglas ex Lehmann (see comments in Results section). $n=22$ —OR, Douglas Co.: Boomer Hill (W), *JSS and R. Holmes* 767.

P. heterophylla Pursh ssp. *virgata* (E. Greene) Heckard. $n=11$ —OR, Douglas Co.: Cow Creek, 714; Elk Creek, *JSS and M. Nelson* 728.

tetraploid individuals; the Elk Creek population also contains diploids. Thus, all seven species in the *P. magellanica* complex that occur as basic diploids are now known to have morphological counterparts at the tetraploid ($n=22$) level.

Two previous tetraploid counts for *P. corymbosa* in Oregon were cited by Heckard (1960). These, plus five additional counts obtained during this study, indicate that *P. corymbosa* may occur primarily at this level in Oregon. Diploids of this species are known to occur in the North Coast Ranges of California, and in one locality in the Sierra Nevada (Heckard 1960).

Three diploid counts for *P. heterophylla* in southwestern Oregon were previously recorded (Heckard 1960). The two additional counts reported here indicate that this species (as ssp. *virgata*) is primarily diploid in Oregon, although it occurs at the tetraploid level elsewhere in its range, mainly as ssp. *heterophylla* (Heckard 1960).

The tetraploid count reported here for *P. hastata* is apparently the first from southwestern Oregon. Although it was initially known only as a tetraploid, diploid individuals of this species have recently been discovered in northern Nevada (L. Heckard pers. comm.). It should be noted that the population identified throughout this paper

TABLE 2. SOIL ANALYSES FROM EIGHT *PHACELIA* SITES IN SOUTHWESTERN OREGON.

Species and population	Soil type	pH	P (ppm)	K (ppm)	Ca meq/100 g	Mg meq/100 g	Ca/Mg ratio	Cu (ppm)	Fe (ppm)
<i>P. capitata</i>									
Beatty Creek	serpentine	7.1	4	35	2.1	12.3	0.17	1.1	74
Boomer Hill (W)	sub-serpentine	6.2	19	82	17.6	7.7	2.3	1.8	124
Bridge	serpentine	6.9	2	140	3.1	20.0	0.16	2.1	64
Elk Creek	serpentine	7.5	1	70	1.7	20.4	0.08	2.4	84
Peel	serpentine	6.7	4	31	1.7	10.4	0.16	0.76	86
<i>P. corymbosa</i>									
Eight Dollar Mtn (N)	serpentine	6.9	1	39	2.5	23.3	0.11	1.7	94
Grave Creek	serpentine	7.2	1	39	2.0	11.5	0.17	1.1	40
<i>P. heterophylla</i>									
Tiller (Elk Creek)	non-serpentine	6.8	34	43	6.3	1.2	5.25	1.5	142

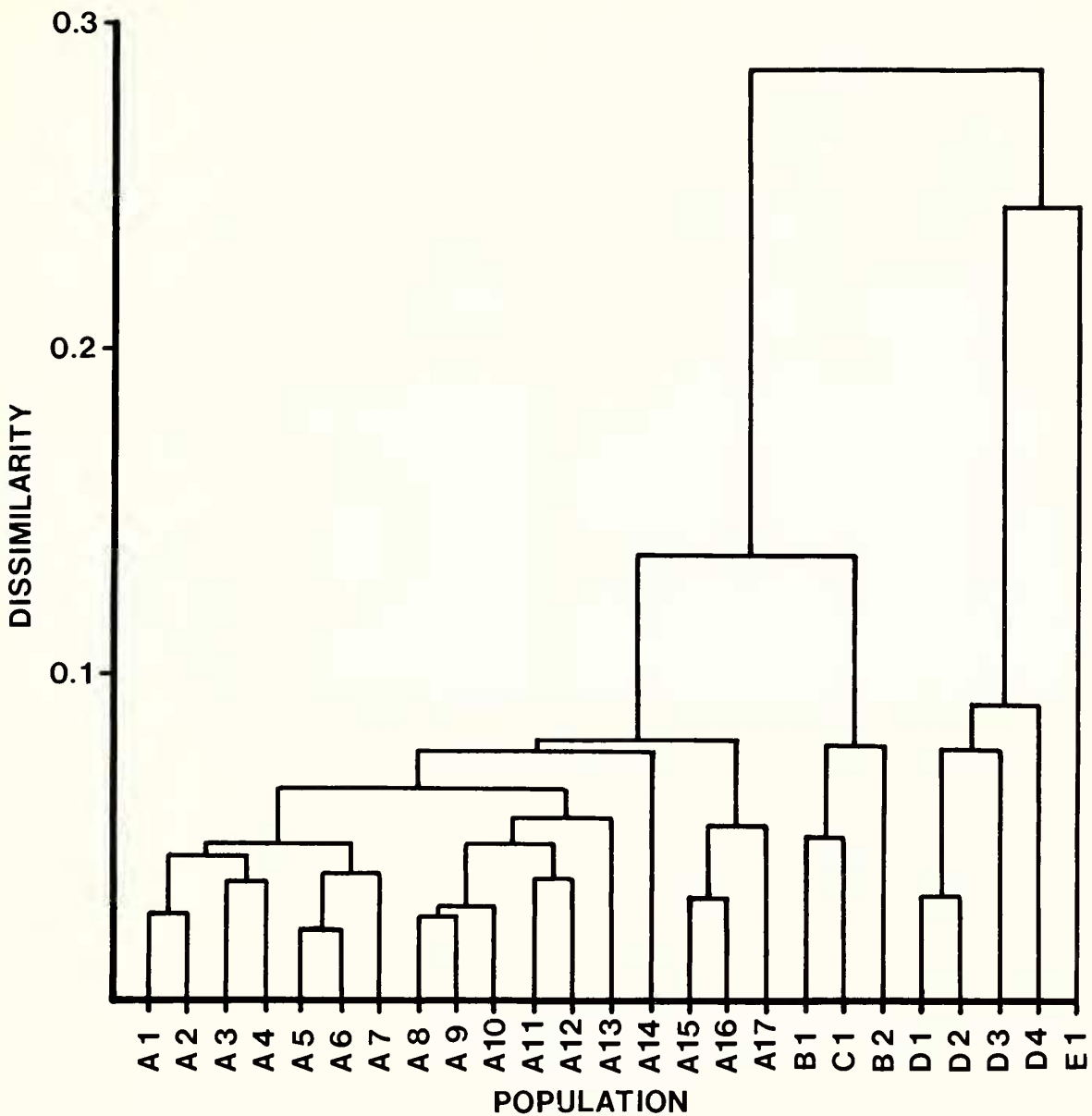


FIG. 2. Cluster analysis of *Phacelia* populations in southwestern Oregon. A = *P. capitata* (2n); B = *P. capitata* (4n); C = *P. hastata* (4n); D = *P. corymbosa* (4n); E = *P. heterophylla* ssp. *virgata* (2n).

as *P. hastata* would represent a range extension for a species whose main distributional range otherwise lies entirely east of the Cascade-Sierra crest (Heckard 1960). It is possible that the parentage of these plants may involve other members of the *P. magellanica* complex, including *P. egena* (L. Heckard pers. comm.). Thus, their identification as *P. hastata* remains speculative at this time.

Morphological studies. The results of the cluster analysis reveal four distinct groups of interest, at a dissimilarity level = 0.12 (Fig. 2). From left to right, these are: 1) diploid *P. capitata* (17 populations); 2) two *P. capitata* populations containing tetraploids, plus the plants suggestive of *P. hastata* (one population); 3) *P. corymbosa* (four populations); and 4) *P. heterophylla* ssp. *virgata* (one population).

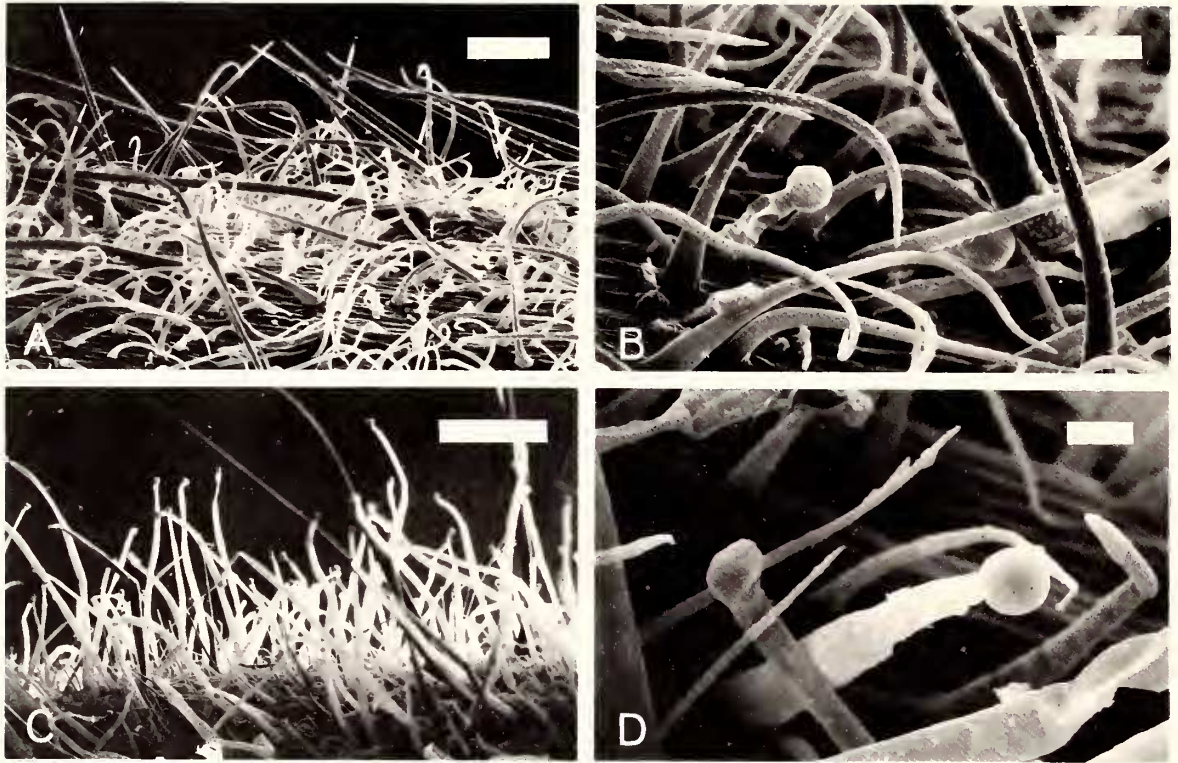


FIG. 3. SEM microphotographs of stem vestiture of *Phacelia capitata* and *P. corymbosa*, taken just below the terminal cyme branches. A, *P. capitata* stem vestiture (scale bar = 100 μm); B, short glandular trichome of *P. capitata* (scale bar = 25 μm); C, *P. corymbosa* stem vestiture (scale bar = 500 μm); D, short glandular trichomes of *P. corymbosa* (scale bar = 25 μm).

Photographs of stem vestiture, taken just below the terminal cyme branches, illustrate the conspicuous medium-length glandular trichomes of *P. corymbosa* (Fig. 3C), which are very important in distinguishing it from *P. capitata* (Fig. 3A). However, *P. capitata* is not eglandular (Fig. 3B) as described by Kruckeberg (1956), but possesses very small glandular trichomes similar to those of *P. corymbosa* (Fig. 3D).

A revised comparison of *P. capitata* with other members of the *P. magellanica* complex in southwestern Oregon is presented in Table 3. A revised description of *P. capitata*, modified from that of Kruckeberg (1956), is presented below.

PHACELIA CAPITATA Kruckeberg, Madroño 13:209. 1956.

Plants deeply taprooted caespitose perennials with 1–many thin, wiry flowering stems each arising from a rosulate tuft of leaves, with numerous sterile leaf rosettes often present. Stems erect, unbranched or occasionally branched, (11–)20–45(–63) cm tall. Herbage finely sericeous, the silvery-gray vestiture consisting of three trichome types: appressed bristles ca. 1–1.5 mm long, underlain by shorter, matted trichomes ca. 0.4–0.5 mm long, and scattered, very short glandular

trichomes, ca. 0.03–0.05 mm long, especially near the inflorescence, on the pedicels, calyx lobes, and leaf veins; long bristles sparse or absent on the lower portion of the stem. Sterile leaves (those in rosettes not subtending flowering stems) linear-lanceolate, simple and entire, very rarely pinnatifid or pinnately compound with 1–2 pairs of basal lobes, (1.7–)2.5–6.5(–8.8) cm long, (2.3–)2.9–6.0(–13.0) mm wide, tapering to petioles 1–2 cm long; climax leaves (those in rosettes at the bases of flowering stems) entire, or occasionally having 1–2 basal lobe pairs; cauline leaves gradually but not wholly reduced upwards. Inflorescences of 2–3 helicoid cymes borne in a congested, capitate or subcapitate cluster, or frequently with 2 or more lateral cyme branches below the terminal cymes; pedicels in early fruit 1–3 mm long, hispid. Calyx lobes linear-oblong, (3.0–)4.2–6.6(–7.7) mm long, 0.5–0.8 mm wide, with long-hispid margins, the abaxial surface short-hirsute. Corollas white, rotate, cylindrical, or occasionally slightly campanulate-spreading, (4.1–)5.0–6.9(–8.0) mm long, (2.3–)3.0–6.0(–8.4) mm broad when fresh, with entire, obtuse-rounded lobes; appendages attached barely a millimeter above the base of the corolla tube, the free portions forming a long (3 mm) and narrow “V” distally; stamens and style exerted 5–7 mm, the filaments glabrous or with a few scattered hairs about mid-length along the filament. Immature capsules ovoid, 2–3 mm long, densely clothed with stout bristles 2 mm long. Mature seeds 1.9–3.0 mm long (in diploid specimens), brown, with reticulate-pitted surface; $n=11, 22$.

DISCUSSION

The *Phacelia magellanica* alliance is an example of a mature polyploid complex. In such complexes, both the morphological and ecological extremes are usually represented by the diploid species. However, the diploids are often less common than the polyploids; their ranges are more restricted, and the amount of genetic variation within their populations is usually less. In addition, the diploids are usually allopatric, or sympatric only in restricted areas, so that the likelihood of hybridization and doubling of chromosome number is much reduced (Stebbins 1971).

In the *P. magellanica* complex, superimposed on a series of seven diploid ($n=11$) species is an interfertile complex of tetraploids ($n=22$) and a few hexaploids ($n=33$). At the time of his study, Heckard (1960, p. 33) stated that each of the basic diploid species, except *P. capitata*, has a “. . . morphologically similar counterpart on the tetraploid level which intimately associates it with the superstructure of intergrading tetraploids.” This group is now known to include *P. capitata*. Heckard (1960) emphasized that the intergradation between polymorphic tetraploid species, often accom-

TABLE 3. COMPARISON OF *PHACELIA CAPITATA*, *P. CORYMBOSA*, *P. HASTATA*, AND *P. HETEROPHYLLA* SSP. *VIRGATA* IN SOUTHWESTERN OREGON.

Species	Chromosome number (<i>n</i>)	Habit	Stem height (cm)	Leaf size	
				Length (cm)	Width (mm)
<i>P. capitata</i>	11, 22	perennial, mat-forming	20-45	2.5-6.5	2.9-6.0
<i>P. corymbosa</i>	22	perennial, mat-forming	7.5-25	2.4-5.2	6.0-14.0
<i>P. hastata</i>	22	perennial, with 1-many stems, rarely mat-forming in this region	20-50	3.5-7.5	7.0-13.0
<i>P. heterophylla</i> ssp. <i>virgata</i>	11	biennial	30-75	3.8-8.0	8.0-17.0

TABLE 3. CONTINUED.

Leaf outline	Inflorescence	Corolla shape	Glandulosity
linear-lanceolate, entire; rarely, with 1-2 pairs of leaflets at base of lamina	cymes often terminal or sub-terminal, or with 1-many lateral inflorescences below the terminal cymes	cylindric (campanulate in tetraploids)	scattered, very short glandular trichomes, especially near the inflorescences, on the pedicels, calyx lobes, and leaf veins
linear to lance-oblong, entire, or often with 1-2 pairs of leaflets at base of lamina	cymes terminal, or often with 1-2 subterminal cyme branches	cylindric-campanulate	conspicuously glandular overall, with short-medium glandular trichomes
lanceolate, entire, or rarely with 1-3 leaflets	cymes terminal or sub-terminal, often with 1-many lateral inflorescences below the terminal cymes	cylindric-campanulate	scattered, short glandular trichomes, especially near the inflorescences, on the pedicels, calyx lobes, and leaf veins
pinnately dissected, with 1-4 pairs of lobes	virgate, with 10-many overlapping lateral cymes	cylindric-slightly flaring	medium-length glandular trichomes frequent in the upper portions of the inflorescence

panied by introgression, has led to very complicated, and sometimes indecipherable, patterns of variation in the *P. magellanica* complex. This is especially true, he states (Heckard 1960, p. 33), because “. . . the initial differences are not of a magnitude to furnish characters which can be conveniently measured. The result of this intergradation is an extensive assemblage of interrelated plants within which lines must be drawn somewhat arbitrarily in order to delimit taxonomic units.”

Of the seven species in the *P. magellanica* complex that occur predominantly or partially as diploids, two were considered in detail in this study: *P. capitata* and *P. corymbosa*. Each of these is a good example of a “morphological and ecological extreme,” having very distinct morphological characteristics and special ecological attributes in the form of virtually complete restriction to serpentine soils. However, of all seven species that are now known to occur at both the diploid and tetraploid levels in the *P. magellanica* complex, *P. capitata* has the most restricted geographical range.

Phacelia capitata was found growing sympatrically with other members of the *P. magellanica* complex at only two locations. The only instance of biotic sympatry with another member of the group was found at the Boomer Hill (west) site, where, as described above, it occurs along a roadbank in a mixed population with the plants resembling *P. hastata*. Chromosome counts from this site showed that *P. capitata* occurs as a diploid and that the *P. hastata*-like plants are tetraploids, a situation that ordinarily limits the formation of fertile interspecific hybrids. Some collections (i.e., *Shelly and Holmes* 768, 771, OSC) are intermediate, however, in their possession of relatively narrow, predominantly entire, silvery leaves. Attempted chromosome counts for these intermediate plants were unsuccessful, as all the buds were past meiosis. On the basis of their morphological intermediacy, however, it appears that hybridization occurred in the past. Of interest at this site is the less stringent nature of the soil, which is intermediate between the highly serpentinized habitats to which *P. capitata* is otherwise restricted, and a non-serpentine soil profile. This, plus the disturbed nature of the roadside habitat, are possibly the factors which allowed *P. capitata* and the *P. hastata*-like plants to become sympatric here.

The Elk Creek population of *P. capitata*, containing diploids and tetraploids, further exemplifies the problems involved in determining the origins of hybrid individuals in the *P. magellanica* complex. On the basis of field observations, the most likely other diploid species involved in this intergradient population is *P. heterophylla*. This species is neighboringly sympatric with *P. capitata*, occurring on non-serpentine soils along the highway both north and south of the serpentine outcrops above Elk Creek. Surveys throughout the

area did not reveal any other morphologically distinct members of the *P. magellanica* complex. Numerous *P. capitata* plants at both Elk Creek and the nearby Callahan Creek site are morphologically suggestive of past hybridization with *P. heterophylla*, particularly in the possession of pinnately compound leaves, which are characteristic of the latter species.

The cluster analysis upholds the morphological distinctiveness of diploid populations of *P. capitata* in comparison with *P. corymbosa* ($4n$), *P. hastata* ($4n$), and *P. heterophylla* ($2n$). The clustering of the two tetraploid *P. capitata* populations with the tetraploids resembling *P. hastata* is most likely due to similar tendencies toward longer, entire leaves, larger corollas, similar stem height, and an intermediate degree of glandulosity amongst the individuals.

Despite the evidence for past genetic interaction of *P. capitata* with *P. heterophylla* and with plants resembling *P. hastata*, it is appropriate to interpret these instances of limited interspecific gene exchange as exceptional events. *Phacelia capitata* remains a unique entity in the *P. magellanica* complex, as evidenced by the morphological, ecological, and almost wholly diploid cytological distinctiveness of the species.

Although the exact evolutionary history of *P. capitata* remains unknown, it seems most appropriate to categorize it as a serpentine neoendemic species. Such species are newly arisen "insular" taxa, often demonstrating a pattern of adaptive radiation into specialized habitats (Kruckeberg 1984). Additionally, because *P. capitata* would have evolved at the diploid level within the *P. magellanica* complex, it conforms well to the diploid speciation model for the establishment of an edaphic endemic species as described by Kruckeberg (1986). In this scheme non-serpentine populations, which may be preadapted for serpentine tolerance, give rise via disruptive selection and subsequent genetic divergence and isolation to new biological species.

The extent to which this process involved a diploid ancestor shared with *P. corymbosa*, if any, is enigmatic. In fact, no very close relative of *P. capitata* is apparent within the *P. magellanica* complex. No evidence of genetic interaction between *P. capitata* and *P. corymbosa* was found, despite their virtually complete restriction to similar serpentine substrates. The two species were found to be fully allopatric, *P. capitata* replacing *P. corymbosa* on the northeasternmost ultramafic outcrops in southwestern Oregon. In addition, *P. corymbosa* is not known to occur as a diploid in Oregon. The northernmost known diploid location for *P. corymbosa* is in Siskiyou County, California, approximately 175 km south of the southernmost location of *P. capitata* (Heckard 1960). Lastly, the two species are both distinct morphological entities in the *P. magellanica* com-

plex, and are very different from one another. If a common diploid ancestor was shared by the two species, it appears to have long been extinct.

Field studies revealed that in many places *P. capitata* has increased in abundance following habitat disturbance. Owing to this ruderal response, the species is not currently threatened or endangered with extinction. It is still important, however, to protect undisturbed populations of such narrowly endemic species so that features of their population ecology, habitat requirements, and evolutionary uniqueness may be studied in natural environments.

ACKNOWLEDGMENTS

This study was completed in partial fulfillment of the requirements for the degree of Master of Science, Oregon State University. I thank Kenton Chambers for his guidance. Support, research, and travel funds were provided by the Department of Botany and Plant Pathology and the Oregon State University Herbarium. Field assistance from Mark Nelson and Russ Holmes, and helpful advice from Robert Meinke, is gratefully acknowledged. LaRea Johnston assisted in the preparation of the photographs. Ginger King provided invaluable assistance in the preparation of the figures. I thank the Editor, L. R. Heckard, A. R. Kruckeberg, and an anonymous reviewer for helpful comments on the manuscript.

LITERATURE CITED

- BERG, M. G. and E. H. GARDNER. 1978. Methods of soil analysis used in the Soil Testing Laboratory at Oregon State University. Agricultural Experiment Station, Corvallis. Special Report No. 321.
- BOESCH, D. F. 1977. Application of numerical classification in ecological investigations of water pollution. U.S. Environmental Protection Agency, Corvallis, Oregon. Ecological Research Series Report No. EPA-600/3-77-033.
- HECKARD, L. R. 1960. Taxonomic studies in the *Phacelia magellanica* polyploid complex. Univ. Calif. Publ. Bot. 32:1-126.
- KENISTON, J. A. 1978. Program CLUSTER: an aid to numerical classification. Oregon State University, Marine Science Center, Newport (unpubl.).
- KRUCKEBERG, A. R. 1956. Notes on the *Phacelia magellanica* complex in the Pacific Northwest. Madroño 13:209-221.
- . 1969. Plant life on serpentinite and other ferromagnesian rocks in northwestern North America. Syesis 2:15-114.
- . 1984. California serpentines: flora, vegetation, geology, soils, and management problems. Univ. California Press, Berkeley.
- . 1986. An essay: the stimulus of unusual geologies for plant speciation. Syst. Bot. 11:455-463.
- OREGON NATURAL HERITAGE DATA BASE. 1987. Rare, threatened, and endangered plants and animals of Oregon. The Nature Conservancy, Portland.
- PROCTOR, J. and S. R. J. WOODSELL. 1975. The ecology of serpentine soils. Adv. Ecol. Res. 9:255-366.
- SNOW, R. 1963. Alcoholic hydrochloric acid-carmin as a stain for chromosomes in squash preparations. Stain Tech. 38:9-13.
- STEBBINS, G. L. 1971. Chromosomal evolution in higher plants. Edward Arnold Ltd., London.
- U.S. DEPARTMENT OF INTERIOR. 1985. Endangered and threatened wildlife and plants; review of plant taxa for listing as endangered or threatened species; notice of review. Federal Register 50:39525-39584.

- WELLS, F. G. and D. L. PECK. 1961. Geologic map of Oregon west of the 121st meridian. U.S. Geol. Survey Misc. Geol. Inv. Map I-325.
- WHITTAKER, R. H. 1954. The ecology of serpentine soils. IV. The vegetational response to serpentine soils. *Ecology* 35:275-288.
- . 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30:279-338.

(Received 8 Aug 1988; revision accepted 28 Jun 1989.)

ANNOUNCEMENT

SECOND ANNUAL CONFERENCE

THE SOCIETY FOR ECOLOGICAL RESTORATION

The Society for Ecological Restoration announces its second annual conference, to be held at the Sheraton International Hotel, at O'Hare, in Chicago, 29 April-3 May 1990. The program will include several special sessions to explore the state of the art as it applies to key environmental issues, and a full program of contributed papers and posters, special lectures, workshops, field trips, and other special events designed to facilitate communication among restorationists and with decision makers and the general public.

Special programs will include: Prairie Restoration, Restoration and Global Climate Change, Setting Standards for Monitoring Restoration Projects, Restoration and Recovery of Endangered Species, and Restoration Philosophy. Field trips will include visits to the prairie restoration project at Fermi National Laboratory, the Des Plaines River and wetland restoration project, Indiana Dunes National Lakeshore projects, Chicago's urban prairies, and the University of Wisconsin Arboretum and Society offices in Madison.

The Society invites submission of abstracts of papers dealing with all aspects of ecological restoration. Special consideration will be given to papers directly related to the special sessions listed above, but papers dealing with any aspect of ecological restoration are welcome. These may include political, administrative, social, economic, and philosophical, as well as purely scientific and technical aspects. Forms for submission of abstracts may be obtained from the Society's office: S.E.R., 1207 Seminole Highway, Madison, WI 53711, (608) 263-7889. The deadline for submission of Abstracts for Contributed Papers is 15 January 1990.